

Relationship of Wood-Feeding Insects and Coarse Woody Debris

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Abstract

Wood-feeding insects serve as food for vertebrates and invertebrates, condition the habitat for later successional organisms, disperse a variety of organisms, and, in some cases, generate coarse woody debris (CWD). This discussion is limited to insects that actively bore into and derive nutrients from the phloem or xylem and are probably important to decomposition. The majority of these insects are in the order Coleoptera, but several other orders are represented. Although a large amount of literature exists, most of it focuses on relatively few, commercially important insects and provides little information about their role in CWD decomposition, nutrient cycling, and energy transfer. More is known about the influence of geographic area, tree species, type of tree tissue, moisture, temperature, size of woody material, and fungal communities on wood-feeding insects.

Introduction

Wood-feeding insects represent a large portion of the fauna that inhabit dead and dying trees. They provide food for vertebrates and invertebrates; alter the habitat, making it acceptable for subsequent inhabitants; serve as transport for a variety of organisms; and, in some cases, are responsible for generating coarse woody debris (CWD).

In choosing the insects to include in this discussion, I needed to define wood-feeding insects and considered a number of questions. For example, are species that feed on phloem and obtain their nutrients from the cell contents, rather than cellulose, wood-feeders? Should insects that bore into wood but rely on externally growing symbiotic fungi for food be included? Should those species that ingest wood fibers but require nutrients or enzymes from ingested microorganisms to complete development be considered? Are insects that rely on gut-inhabiting symbiotic protozoa to digest cellulose wood-eaters?

These questions point to the many ways insects have evolved to take advantage of the energy stored in trees. I chose a broad definition that is not based on where the microorganisms that aid in digesting the wood are located, because almost all wood-feeding species have some symbionts that help them use wood as a food source. However, I restricted the discussion to insects that actively bore into and derive nutrients from the phloem or xylem

(wood) of trees in terrestrial habitats and are likely to be important in the decomposition process.

Wood-feeding insects occur in many orders of the class Insecta, from the primitive eusocial termites to the more highly evolved Hymenoptera; however, the majority are Coleoptera. Individual life histories and habits of the wood-feeding groups or species is beyond the scope of this paper. Readers can find this information elsewhere (Anderson 1960; Barbosa and Wagner 1989; Coulson and Witter 1984; Drooz 1985; Hickin 1976). In addition to the life history and habits of the economically important wood-feeding insects and their associates, some researchers have looked at the community and successional patterns of insects in woody debris (Blackman and Stage 1918, 1924; Elton 1966; Fager 1968; Graham 1925; Howden and Vogt 1951; Savely 1939; Townsend 1886). Despite this large body of excellent work on a number of CWD inhabitants, little attention has been given to how insects affect decomposition, nutrient cycling, or energy flow in this habitat.

The following discusses the principal groups of insects feeding on CWD in the South, their roles in CWD, and how CWD habitat affects insect communities and vice versa.

Wood-Feeding Insects

Most of the information on wood-feeding insects focuses on those species that cause economic injury to trees or damage wood products. As a result, literally thousands of publications have been written about termites and bark beetles, while little information is available on the wood-eating Tenebrionidae, Elateridae, or Alleculidae. The appendix presents a partial listing of wood-feeding species in the South, their habits (phloem vs. xylem feeders, branch vs. bole inhabitants, etc.) and their host associations. Compiling the appendix was relatively easy for the economically important families. However, as Elton and Miller (1954) discovered 40 years ago, I found that an incredible number of species have been described taxonomically, but with no description of their "ecological setting and context." Therefore, the wood-feeding members of some of the largest families are not included because either larval host records are scattered or do not exist, or their function within the larval habitat has not been defined.

Order Dictyoptera—Cockroaches

Family Cryptocercidae. This family contains one species, *Cryptocercus punctulatus*, which occurs in moist rotted logs, particularly oak. Entomologists are interested in this reddish brown, wingless insect because it serves as a phylogenetic link between roaches and termites. Like termites, *C. punctulatus* harbors xylophagous protozoa that help with digestion of its wood fiber diet (McKittrick 1964, 1965). Little is known about its relationship to CWD, although it is not likely to be important in decomposition.

Order Isoptera—Termites

Only 8 of the 2,100 species of termites are found in more than one or two Southern States, and only 4 species are common throughout the South. Despite the relatively small number of termite species, they are probably one of the dominant components of southern forest ecosystems that influence the decomposition of CWD. Termites are important to man throughout the world, and receive considerable attention and study as demonstrated by the extensive bibliographies compiled by Snyder (1949, 1961, 1968) and Ernest (1986). This literature deals primarily with the biology and control of termites, while relatively little attention has been directed at their ecological role in the temperate forests of North America (Lee and Wood 1971; Lobry de Brun and Conacher 1990).

Termites are social insects forming colonies usually produced by a single mated pair. Colonies may be composed of a king and queen (primary reproductives), supplementary reproductives, immatures, nymphs, soldiers, workers, and alates or winged reproductives (Weesner 1965). Alates initiate new colonies following reproductive flights that occur during specific times of the year. The timing of these flights depends upon the species. Males and females pair during the flights, prepare copularia in suitable habitats, mate, and begin producing young. As the newly produced apterous nymphs mature, they form the worker caste of sterile terminal form (no longer molting) individuals that, along with the nymphs, undertake all aspects of colony care and construction. Soldiers are also sterile, mature individuals that must be fed by workers and, as their name implies, are responsible for colony defense. Supplementary reproductives either replace the queen when she dies, or, in some species, supplement the buildup of the colony population. Alates, or winged reproductives that are produced in large numbers during certain seasons, are not found in the colony at other times (Krishna and Weesner 1969; Weesner 1965).

Termites in the Southern United States primarily feed on cellulose from wood. Lower-order termites have flagellate protozoans in their gut to aid in cellulose digestion, while the Termitidae rely on symbiotic bacteria (Wood 1978). The wood of most trees is acceptable food for termites (Wood 1978), so the appendix does not list hosts for the Isoptera. However, termite species show distinct preferences for specific woods (Smythe and Carter 1969) and in some cases prefer wood infected by specific fungi (Smythe and others 1971). The presence of other fungi may result in termite rejection of the wood as a food source or in poor termite survival (Becker 1969; Smythe and others 1971).

Wood density is also a factor in food preference. Soft fast-growing springwood is usually preferred over denser latewood. This preference frequently results in thin layers of latewood remaining in logs where the more preferred earlywood has been excavated.

Termites are a relatively small group with two families represented in the South (appendix). The drywood termites (Kalotermitidae) are predominately found in Florida, although several species are more widely distributed. The subterranean termites in the family Rhinotermitidae include the most common species, *Reticulitermes flavipes* and *R. virginicus*. A third subterranean species, the Formosan termite *Coptotermes formosanus*, was introduced into Louisiana and is now widely distributed in the South. This non-native species consumes wood at a faster rate and also infests wood of living trees. Its potential impact on the forested ecosystems of the South has not been investigated.

Termites are a ubiquitous component of the decomposer community in the South, which has been studied extensively. Their ecosystem roles have been considered in other parts of the world as well (Wood 1976, 1978; Lee and Wood 1971; Gentry and Whitford 1982; Lobry de Brun and Conacher 1990). However, considering their potential importance in CWD and soil modification, the role of subterranean termites in these processes has been neglected in the Southern United States.

Order Coleoptera—Beetles

The order Coleoptera, the largest in the Class Insecta, has over 30,000 species in the United States (Borror and others 1976). Twenty-four of the 110 families represented in the United States and described by Arnett (1968) include terrestrial wood-feeding species. However, only in the

relatively small families (e.g., Platypodidae) are all members wood-feeders. The appendix contains a partial listing of the wood-feeding Coleoptera in the South. This list includes species that attack living and dead trees, those that feed on phloem or xylem tissue, and those that feed on wood in its last stages of decomposition. A large percentage of the xylophagous species rely on gut-inhabiting microfauna for the partial breakdown of cellulose. I have also included the ambrosia beetles; those species inoculate their galleries in wood with specific fungi on which the larvae feed. The inclusion of insects feeding in well-rotted logs is arbitrary, because many of these species derive part or all of their nutrition from fungi and other microorganisms that they ingest with the wood fibers. However, they are important in fragmentation of CWD (Ausmus 1977) and may contribute to incorporation of decomposed wood into the soil.

A number of beetles attack living trees where they feed on xylem tissue. These insects play at least two roles relating to CWD. First, they weaken trees structurally, making them more susceptible to breakage and resulting in CWD input. Second, they contribute to the decomposition of CWD by opening the tree bole to invasion by fungi and other organisms before the tree dies, resulting in CWD that is well advanced in decomposition before it even enters the detritus food web.

The appendix does not contain species lists for the families Elateridae, Tenebrionidae, Alleculidae, and Melandryidae, even though these families probably contain wood-feeders (Arnett 1968). Species descriptions in these families are frequently based on adult insects often caught by means that provide no information on the larval habits. Therefore, host records, if they exist, give no useful information in regard to CWD.

Families Lucanidae, Passalidae, and Scarabaeidae.

During the larval stage, the C-shaped white grubs of these families are similar in appearance. Richter (1966) provided keys to the larvae and brief descriptions of the biology of some of the common species. Larvae of all three families are found in well-rotted logs. Lucanids and scarabs are solitary, while the passalids form loose social groups in which the adults feed chewed wood mixed with saliva to the larvae (Gray 1946). Because they are large, these insects may be important in both direct and indirect CWD fragmentation.

Families Buprestidae and Cerambycidae. The flatheaded or metallic wood borers (Buprestidae) and the long-horned wood borers (Cerambycidae) are large, diverse families that

contain some of the most common and important wood-feeding species. Franklin and Lund (1956) compiled the species of Buprestidae that occur in Georgia, which include the common Southern species. Linsley (1961, 1962a, 1962b, 1964) and Linsley and Chemsak (1972, 1976, 1984) revised most of the subfamilies of Cerambycidae and provided biological information on species when available. A number of species are common in recently killed trees, where they often feed initially on phloem and then enter the sapwood or heartwood to complete their development. Others feed exclusively on wood in conditions ranging from wood of live trees to wood in the final stages of decomposition. Some attack stumps and boles while others occupy only branches of certain size classes. Both families contain species that attack living trees, either weakening or killing them, while some species contribute to woody debris input by girdling or pruning twigs or branches. More detailed accounts of common injurious species are provided by Drooz (1985) or Coulson and Witter (1984).

Families Elateridae, Tenebrionidae, Alleculidae, and Melandryidae. Little is known of the larval habits of these families, although adults and larvae of some species are found in CWD. Some of the elaterids or click beetles found in CWD are known predators, while others are probably wood-feeders (Arnett 1968).

Family Curculionidae. Despite the large size of this family, relatively few weevils can be classified as wood-feeders. However, several are commonly associated with CWD in the South. These include the Pales and pitch-eating weevils, *Hylobius pales* and *Pachylobius picovorvus*, and the deodar weevil, *Pissodes nemorensis*, which feed on the phloem of recently killed pine tree boles, stumps, and roots. The remaining species are also primarily phloem feeders on a variety of host species, although a few weevils feed on rotten wood and some bore into sound wood.

Families Anobiidae, Lyctidae, and Bostrichidae. These families are grouped together because all the species found in CWD are xylophagous, and most are capable of feeding on, or prefer, relatively dry wood. Because the wood-feeding larvae of these three families pack their tunnels with a fine powderlike boring dust and frass, they are labeled "powder-post beetles," a name officially applied to the Lyctidae. These beetles are likely to occur where other wood-feeding species are rare, such as standing dead trees on xeric sites or dead limbs still attached to trees, because they are able to attack relatively dry wood. Some members of the family Curculionidae (subfamily Cossoninae) could also be included in this group.

Families Scolytidae and Platypodidae. The bark beetles, or scolytids, contain a large number of the most important forest pests. They often arrive first at newly created CWD or, in some cases, they contribute significantly to CWD input. These insects are primarily phloem feeders that attack all parts of the tree. A number also bore into wood. Some feed in the lower bole while others feed only in branches of a particular size class. Some species of Scolytidae (tribe Xyleborini) and all of the Platypodidae are ambrosia beetles that feed larvae by inoculating adult-constructed galleries with a mold-type fungus (Graham 1966; Norris 1979). Bark beetles have received considerable attention because they are economically important. In two excellent books, Wood (1982, 1987) has revised the New World species and compiled the literature references on these beetles.

Order Lepidoptera—Moths

Families Noctuidae, Sesiidae, and Cossidae. Moth larvae or caterpillars that feed on wood in the South are found in these three families. Only one species of Noctuidae feeds on wood in the South: *Scolecocampa liburna*, a common species found in rotting logs. The remaining species, in the families Sesiidae and Cossidae, are found in live trees, feeding primarily on wood, although a few are phloeophagous. These species contribute to decomposition of wood before the tree dies, increasing tree susceptibility to wind breakage and disease. Drooz (1985) and Johnson and Lyon (1988) have reviewed the biologies of the important pest species in these families.

Order Hymenoptera—Wasps and Bees

Families Siricidae and Xiphydriidae. Both families in this order bore in wood and have similar habits. Morgan (1968) reviewed the literature on Siricidae, and Smith (1976) revised the literature on xiphydriids of North America with notes on hosts and biology. Although the woodwasps actively bore in wood of very weak or dead trees, they rely on symbiotic fungi inoculated into the tree during oviposition as an aid in digestion (Martin 1987) or possibly as a sole food source (Morgan 1968).

Roles of Wood-Feeding Insects in Coarse Woody Debris

Studies of wood-feeding insects in CWD have focused primarily on CWD as a habitat and on the community structure and successional changes that occur as the wood decomposes (Townsend 1886; Blackman and Stage 1918,

1924; Graham 1925; Savely 1939; Howden and Vogt 1951; Fager 1968; Elton 1966). Very little attention has been given to the effects of wood-feeding insects on the processes of energy flow and nutrient cycling. Despite this lack of study, Harmon and others (1986) show that wood-feeding insects serve important functions in forest ecosystems.

Coarse Woody Debris Input

Insects are just one of many factors contributing CWD to forested ecosystems, where their relative importance in this role depends on forest type (Harmon and others 1986). In the South, pines are the dominant tree species in the Coastal Plain and Piedmont and, as a result of both natural and man-related activities, *Pinus* spp. represent one of the major sources of CWD in this region. Aside from man, the southern pine beetle (SPB) *Dendroctonus frontalis* is one of the primary factors influencing the spatial and temporal arrangement of CWD in southern forests. Price and others (1991) have compiled an excellent historical account of SPB outbreaks with detailed maps of outbreaks over a 30-year period. Their work demonstrates the spatial and temporal variability of CWD input in southern forests. Table 1 shows the temporal changes in CWD resulting from SPB activity across the South. Regional loss figures in table 1 were calculated from the State volume figures provided by Price and others (1991). The number of trees is estimated by calculating the volume of a tree 22-m tall, 50-cm diameter at the butt end, and tapering to a 10-cm diameter top. The volume figure for each year was then divided by the per-tree volume to determine the number of trees. Similarly, the number of hectares of trees killed was estimated by assuming that each hectare contained 178 trees. These data show the potential CWD input from SPB activity, but timber salvage efforts reduced the actual input. For example, in 1980 SPB killed 8.6 million m³ of wood as the equivalent of 5.9 million large trees. However, the amount of wood not salvaged was only 4.0 million m³ or about 47 percent of the total mortality. Without SPB suppression efforts, the figures in table 1 would be much higher, as demonstrated in a potential wilderness area in Texas where SPB killed 1416 hectares of pine, equivalent to 94,400 m³ of wood, before control measures were initiated and the infestation was stopped (Billings 1992).

The SPB is the only wood-feeding insect that causes large-scale forest mortality in the South. However, other species may also be important. Populations of pine engravers (*Ips* spp.) frequently build up in logging slash, windthrown, or lightning-struck trees, and subsequent generations attack healthy trees. Quick decline of these populations usually

Table 1—Potential CWD volume input over an 18-year period resulting from southern pine beetle, *D. frontalis*, activity in the Southern United States, and estimates of the number of trees and hectares of forest affected^a

Year	Volume (m ³)	No. of trees ^b	Hectares ^c
----- millions -----			
1973	6.5	4.4	24,719
1974	6.6	4.6	25,843
1975	6.0	4.1	23,033
1976	3.0	2.1	11,798
1977	1.1	0.8	4,494
1978	0.9	0.6	3,371
1979	6.4	4.4	24,719
1980	8.6	5.9	33,146
1981	0.8	0.5	2,809
1982	2.1	1.4	7,865
1983	0.6	0.4	2,247
1984	0.8	0.5	2,809
1985	8.4	5.8	32,584
1986	7.2	5.0	28,090
1987	1.7	1.2	6,741
1988	4.7	3.2	17,977
1989	1.2	0.8	4,494
1990	0.5	0.3	1,685

^a Compiled from Price and others (1991).

^b Estimates based on average tree 20-m tall, 50-cm diameter at base, and 10-cm diameter at the top.

^c Estimate based on each hectare containing 178 trees.

results in small groups of dead trees (Drooz 1985). Thatcher (1960) reported that pine engraver activity resulted in a loss of 3.7 million m³ of timber in southern forests, while Baker (1972) reported 1.1 million m³ per year of pine mortality due to these beetles in Florida alone. Ips bark beetle may represent a major source of CWD in this region because infestations are usually small and scattered, and salvage is often not economically feasible.

In southern hardwood forests, wood-feeding insects are probably a much less important source of tree mortality. The hickory bark beetle, *Scolytus quadrispinous*, is capable of localized outbreaks that result in significant tree mortality (Beal and Massey 1945; Drooz 1985), and wood-feeding insects serve as vectors of several important and

lethal hardwood tree diseases including oak wilt, *Ceratocystis fagacearum* (Rexrode 1968; Rexrode and Jones 1970), and Dutch elm disease, *C. ulmi* (Carter 1962). Borers that feed on the sapwood or heartwood of live trees contribute indirectly to CWD input in hardwood forests by weakening trees, making them susceptible to wind breakage or disease. Finally, twig and branch pruners and girdlers (table 1) can add small woody debris through their feeding and oviposition behavior.

Vectors and Transport

Wood-feeding insects carry a large array of pathogenic and saprophytic microorganisms as they move from tree to tree. Whitney (1982) provides an extensive list of symbiotes of conifer-killing bark beetles. The list includes 38 genera of fungi, 17 genera of bacteria, and 4 genera of protozoans. These numbers are remarkable only because the survey was limited to the more aggressive tree-killing species of four bark beetle genera.

A number of wood-feeding insects, such as ambrosia beetles and woodwasps, have specific associations with fungi that they carry and use for food. Norris (1979) lists the ambrosia fungi of the Xyleborini beetles (Scolytidae) and the types of mycangia that have evolved in these beetles for carrying their symbiotic fungi. Woodwasps (Siricidae and Xiphydriidae) have similar associations. Morgan (1968) has reviewed the biology of siricids and their fungal symbiotes. Woodwasps use long ovipositors to drill holes 2-15 mm into the wood, where they deposit eggs and the symbiotic fungi upon which the young depend. Fungi associated with woodwasps probably affect CWD decomposition more than those associated with ambrosia beetles.

A number of mite species rely on wood-feeding insects for transport between habitats. Eighteen species of mites are recorded as phoretic on the SPB alone (Moser 1976). Moser and Roton (1971) found 96 species of mites associated with bark beetle-infested trees in Louisiana and listed the subcortical insects that served as phoretic hosts. The long list suggests that most wood-feeding insects carry mites between habitats. Soper and Olson (1963) reported 13 genera of mites associated with *Monochamus* spp. in Maine. The majority were thought to be phoretic.

Nematodes are also carried by wood-feeding insects. Massey (1974) found 51 genera of nematodes that were parasitic on or associated with bark beetles in the United States. Parasitic species were carried internally to new bark beetle habitats, while most of the other species associated

with bark beetles are probably phoretic. Dwinell and Nickle (1989) considered most of the 49 species of mycophagous *Bursaphelenchus* nematodes to be phoretic on wood-borers.

These studies suggest that wood-feeding insects probably carry a much greater number and diversity of organisms than is currently known and, for those organisms, serve as a vital link between habitats.

Exposure of Wood to Other Organisms

Wood-feeding insects not only transport organisms to new CWD habitats, they also create openings and modify CWD so that other organisms can gain access or survive. Entry holes by bark beetles allow other organisms to enter the inner bark. For example, Dowding (1973) found that prevention of bark beetle attacks on *Pinus sylvestris* logs greatly reduced the numbers of Diptera found. A large number of the scavengers and predators associated with SPBs (Overgaard 1968) used openings created by bark beetles to enter the inner bark. For example, some of the 96 species of mites associated with bark beetles in Louisiana entered through holes created by the bark beetles (Moser and Roton 1971). Whitney and Cobb (1972) maintained that beetle tunnels are an important mode of entry for Basidiomycotina and other fungi in ponderosa pine. However, Dowding (1982) questioned the importance of beetle tunnels for fungal colonization by airborne spores, suggesting that other wound sites are more important. Swift and Boddy (1982) state that after ambrosia beetles vacate their galleries the tunnels provide infection courts for nonsymbiotic fungi.

Channelization and Fragmentation

Insects tunnel through CWD by chewing, digesting, and excreting both phloem and xylem. Some species (e.g., powderpost beetles) tightly pack the wood particles and excrement in the larval mines, while others (e.g., termites) clear their galleries. Phloeophagus insects mine the inner bark and cambium extensively and introduce fungi that, in combination with beetle tunneling, loosen the bark, which eventually sloughs off.

Insect feeding in the wood is a direct form of fragmentation. In addition, the combination of insect feeding and fungal decomposition weakens the wood, making it more susceptible to accelerated fragmentation by woodpeckers (Kroll and others 1980) and other vertebrates in search of food (e.g., bears, skunks).

MacMillan (1988) found that fragmentation was a major reason for the disappearance of oak, hickory, and beech CWD in Indiana although the organisms responsible were not identified. The principal channelizers in hardwood logs on mesic sites in Tennessee (termites, carpenter ants, and passalid beetles) regulate the rate of decomposition by altering the substrate and shifting the competitive advantage of microbial colonizers (Ausmus 1977).

Most nutrients are probably transferred out of logs and snags through fragmentation (Harmon and others 1986). Channelization and fragmentation by wood-feeding insects have been implicated in the initiation and acceleration of nutrient loss from decaying branch wood (Swift 1977; Swift and Boddy 1982) and tree boles (Ausmus 1977). However, nutrient loss probably depends on the element involved. For example, nitrogen content is highest in the later stages of decay when CWD is more susceptible to fragmentation. Conversely, potassium content is low due to leaching (Swift 1977) and is less affected by fragmentation (Harmon and others 1986). Although wood-feeding insects play an important role in CWD decomposition and nutrient transfer, few quantitative data are available on their role in leaching or fragmentation losses.

Energy Transfer

The intricate food webs and succession of wood-feeding insects in CWD during decomposition are indicative of the energy release from this resource. I found no quantitative data on this subject, although it is likely that these data could be determined from the literature on bark beetle population dynamics at least for the major tree-killing species of bark beetles and possibly for their parasites and predators. However, similar data are not available for the large majority of the other wood-feeding insects.

Coarse Woody Debris as a Habitat for Wood-Feeding Insects

The wood-feeding insect community is affected by a wide range of factors from geographic location to microclimatic condition. Unlike the role of insects in decomposition processes, the heterogeneity of CWD and its impact on insect communities is understood better. This is particularly true for economically important species, such as bark beetles and termites. Much less is known about the myriad of other species that feed on wood.

Wood-feeding insect communities vary across elevational and latitudinal gradients. A good example of latitudinal differences is termite diversity, which decreases as one moves south to north (Wood and Sands 1978). In the United States, 13 species occur in Florida, while only 1 species has been reported in New Hampshire (Light 1934; Nickle and Collins 1989). Insect diversity also tends to decrease with increasing elevation (Wood and Sands 1978). However, in compiling table 1 it was clear that North Carolina has a number of wood-feeding insects associated with host-tree species unique to the upper elevations of the Southern Appalachian mountains, as well as a number of insects more typically found in northern regions. The higher elevation allows insects to extend their range farther south than is possible along the Coastal Plain. Therefore, oak trees of comparable size dying at the same time in south Georgia, in the upper elevations of North Carolina, and in New Hampshire are likely to have different wood-feeding insect communities. However, the similarity between the North Carolina and New Hampshire trees may be greater than one would predict based on changes in latitude alone.

A number of other factors influence the insect community after a tree dies in a given region. The timing of CWD input influences insects. This is particularly true for the early successional community in phloem and for insects that have only one restricted flight period annually. Xylophagous insects may be less affected by timing because the wood deteriorates more slowly than the phloem. However, termites were found in SPB-killed trees 3 months after death (Barrone 1970). This rapid colonization by termites could exclude other wood-feeding insects that normally arrive later.

One of the most obvious factors affecting insect communities in CWD is tree species. A quick glance at table 1 shows that many wood feeders are restricted to one or a few species of host trees, often within a single genus, while others have broad host ranges. In general, the more restricted host lists indicate those species that arrive during or soon after tree death, while the expanded host lists indicate species using later stages of decay. Those species that arrive early in the decomposition process are often more specialized because they must overcome the plant's secondary or defensive compounds (Käärik 1974; Haack and Slansky 1987). Other insects are capable of utilizing a wide range of tree species but show preference for certain species. For example, termites show distinct preference for certain woods in laboratory bioassays (Smythe and Carter

1969, 1970); however, very little is known about their natural preferences under field conditions (Waller and LaFage 1987).

In addition to differences among species, the resistance of wood to decomposers varies within species (Clark 1957), as well as within individual trees. For example, the sapwood of bald cypress, *Taxodium distichum*, is readily consumed by the Formosan termite, *Coptotermes formosanus*, because it is unprotected by the allelochemicals found in the heartwood (Scheffrahn and others 1988).

The position of CWD can also affect wood-feeding insects. Howden and Vogt (1951) found considerable differences between the insect communities in standing dead pines compared to felled trees (Savely 1939). However, the differences noted could have resulted from other factors, such as temporal and spatial differences or tree species. The location of woody debris on mesic or xeric sites (Abbott and Crossley 1982) or on slopes with different aspects can affect CWD moisture content and decomposition process (Mattson and others 1987) and probably the insect community as well.

The moisture content of logs is a critical factor in shaping CWD communities, as Graham (1925) demonstrated for the cerambycids *Asemum* sp. and *Monochamus* sp. Likewise, the termite *C. formosanus* preferred wood with the highest initial moisture content (Delaplane and LaFage 1989). Other wood-feeding insects show a preference for, or an ability to use, dry wood (e.g., Lyctidae).

Wood temperature may also affect insect community development in CWD. For example, Graham (1925) found that the buprestid *Chrysobothris dentripes* occurred on the tops of logs exposed to direct sunlight, and Savely (1939) demonstrated that a *Chrysobothris* sp. had a tolerance for high temperatures that excluded other species. Therefore, insect communities of logs or snags exposed to direct sunlight may differ from those in shaded areas or on north-facing slopes.

The size of CWD can affect insect community composition. Table 1 clearly demonstrates that some beetle species prefer small branches, while others attack only the base of trees (e.g., *Dendroctonus terebrans* or *Platypus flavicornis*). Some wood-feeding termites also prefer large logs while others feed on small branches (Wood 1976).

Fungi play a key role in the use of CWD by certain insects. Some insects are dependent on fungi for food and have developed very specific associations, e.g., ambrosia beetles and woodwasps. In addition to species that rely on specific fungi, many wood-feeding insects are affected by the fungal community in CWD in a variety of ways. Swift and Boddy (1982) provide a detailed discussion of the interaction between fungi and insects.

Fungi contribute to the nutritional ecology of wood-feeding insects in several ways. First, the fungi contribute nutrients for insect development not found in sufficient amounts in wood alone; in particular, nitrogen and other elements are concentrated in fungal mycelia (Swift 1977, 1978). Second, fungi partially break down or digest the wood, leaving behind a softer, more chewable resource that may be more readily assimilated (Swift and Boddy 1982). For example, *Reticulitermes flavipes*, a common subterranean termite species in the Eastern U.S., preferred and survived better on wood decayed by a number of brown-rot fungi (Smythe and others 1971). Third, fungi increase the moisture content of decaying wood, which may alter its acceptability as a habitat and food source for some wood-feeding insects. Fourth, enzymes produced by fungi and ingested by insects with the wood they eat provide yet another benefit. Martin (1987) reviewed the literature on ingested fungal enzymes and suggested that ingested enzymes will prove to be responsible for cellulose digestion in the xylophagous members of the Cerambycidae, Buprestidae, and Anobiidae families. Finally, fungi are important in detoxifying wood that contains toxic or repellent allelochemicals. Swift and Boddy (1982) summarize several studies that demonstrated termites' use of wood when fungi reduced the quantity of allelochemicals present.

Fungi can also have a negative effect on insects. Becker (1969) found that pine stumps decayed by white-rot fungi were usually free of termites, and Amburgey and Beal (1977) showed that the white-rot fungus *Ganoderma applanatum* inhibited feeding by *Reticulitermes* spp. on infected wooden stakes. Smythe and others (1971) demonstrated reduced survival for *R. flavipes* on wood decayed by *Poria cocos* and *P. monticola*.

It is evident from this brief discussion that wood-feeding insect communities in CWD are shaped by a number of factors; and, as a result, the composition of these communities may vary considerably depending upon the combination of conditions in which the CWD is produced and decomposes.

Summary

Wood-feeding insects are a major component of the diversity of organisms associated with CWD and southern forests. Their feeding activity alters the habitat, they carry with them a wide array of organisms from bacteria to mites that further influence the environment and decomposition process, and they provide openings and food for complexes of other organisms. As a result of these activities, wood-feeding insects have a significant impact on CWD decomposition and the communities of organisms involved. Conversely, the wood-feeding insects are affected by a number of physical and biological factors that determine their ability to use CWD.

Despite the obvious activity and abundance of wood-feeding insects in CWD, few have been studied. Those studied extensively are predominantly pest species that occur early in community succession on CWD, attack living trees, or affect structural wood. These studies have focused on basic insect biology and control with little or no emphasis on the role insects play in the decomposition process. In general, studies on CWD decomposition have not considered the role of insects (Harmon and others 1986). Those that have done so, have often dealt with small branch wood (e.g., Abbott and Crossley 1982; Swift and others 1976) or failed to identify the insect community structure or abundance. However, Ausmus (1977) considered insects in studies of large woody debris and concluded that they were a key component regulating decomposition.

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